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**A review of predator-prey and
competitive inter-specific interactions
in Atlantic salmon (*Salmo salar*)**

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**Examen des relations prédateur-proie
et des interactions interspécifiques
chez le saumon atlantique (*Salmo
salar*)**

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FOREWORD

This document is a product from a workshop that was not conducted under the Department of Fisheries Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process. It is one of a number of contributions first tabled at a DFO-SARCEP (Species at Risk Committee / Comité sur les espèces en péril) sponsored workshop in Moncton (February 2006) to begin the development of a 'Conservation Status Report' (CSR) for Atlantic salmon. When completed in 2007, the CSR could form the basis for a Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report, recovery potential assessment and recovery strategy, and most importantly, enable DFO to implement pre-emptive management measures prior to engagement in any listing process.

AVANT-PROPOS

Le présent document est issu d'un atelier qui ne faisait pas partie du processus consultatif scientifique du ministère des Pêches et des Océans, coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif. Il fait partie des nombreuses contributions présentées au départ lors d'un atelier parrainé par le MPO-SARCEP (*Species at Risk Committee / Comité sur les espèces en péril*) à Moncton (février 2006) en vue de commencer l'élaboration d'un rapport sur la situation de la conservation du saumon atlantique. Lorsqu'il sera terminé, en 2007, ce rapport pourrait servir de base à un rapport de situation du Comité sur la situation des espèces en péril au Canada (COSEPAC), à une évaluation du potentiel de rétablissement et à un programme de rétablissement mais, avant tout, il permettra au MPO de mettre en œuvre des mesures de gestion anticipées avant même de s'engager dans un processus d'inscription.



ABSTRACT

This paper reviews Atlantic salmon (*Salmo salar*) feeding behaviour, prey, predator relations, and competitive interactions. Juvenile salmon feed heavily in spring, less heavily in summer and fall, and minimally in winter. Diurnal feeding cycles are variable in summer, but in winter juveniles are nocturnal. Juvenile Atlantic salmon typically feed by darting up from home stations to seize passing prey. Juveniles in streams feed on aquatic invertebrates, including Ephemeroptera, Plecoptera, Trichoptera, Chironomiidae, and Coleoptera. Smolts on their downstream migration also feed on aquatic invertebrates. Growth in marine waters is much more rapid than in stream habitat. Marine-phase Atlantic salmon feed most heavily in spring. Post-smolts eat mostly invertebrates, while larger salmon eat a higher proportion of fish. Marine-phase salmon occupy the middle and upper layers of the water. Capelin, sand lance, herring, and a variety of crustaceans are among the principal foods of marine-phase salmon in the Northwest Atlantic. Atlantic salmon eggs may be consumed by ducks and by Atlantic salmon. Atlantic salmon fry and parr are consumed by birds, particularly common mergansers, belted kingfishers, and double-crested cormorants, and fish, including Atlantic salmon, trout, eels, and smallmouth bass. Under predation threat juvenile Atlantic salmon either freeze, relying on cryptic coloration, or dash for cover. Outmigrating smolts may be eaten by cormorants and other birds, seals, and by a variety of fish. In the open sea salmon are taken by predatory fish, birds, and seals. Adult salmon returning to their native rivers are subject to seal predation. Atlantic salmon in freshwater compete for resources with conspecifics and with other species, particularly other salmonids. Atlantic salmon competitively displace brook and rainbow trout from riffle habitat, but trout are stronger competitors in slow water. Wintering juvenile Atlantic salmon require rocky cavities for daytime shelter, which may be subject to intense inter- and intra-specific competition. In the ocean, competitive interactions between Atlantic salmon and other species have not been experimentally investigated. It is unlikely that nutrient flux due to Atlantic salmon contributes significantly to freshwater productivity.

RÉSUMÉ

Le présent document traite du comportement alimentaire, des relations prédateur-proie et des interactions biotiques chez le saumon atlantique (*Salmo salar*). Les saumons juvéniles s'alimentent davantage au printemps qu'en été et qu'à l'automne et très peu en hiver. Leurs cycles d'alimentation diurne varient durant l'été, mais les saumons juvéniles sont nocturnes en hiver. Typiquement, les saumons atlantiques juvéniles attendent que des proies passent devant leur repère pour s'élançer sur elles. Dans les cours d'eau, les saumons juvéniles se nourrissent d'invertébrés aquatiques, y compris d'éphéméroptères, de plécoptères, de trichoptères, de chironomes et de coléoptères. Durant leur descente vers la mer, les saumoneaux se nourrissent également d'invertébrés aquatiques. La croissance en eaux marines est beaucoup plus rapide que celle en cours d'eau. En mer, les saumons atlantiques s'alimentent le plus au printemps. Les post-saumoneaux se nourrissent principalement d'invertébrés, tandis que les plus gros saumons capturent une plus forte proportion de poissons. En mer, les saumons occupent les couches d'eau moyennes et supérieures. Parmi les principaux aliments du saumon dans les eaux de l'Atlantique Nord-Ouest, mentionnons le capelan, le lançon, le hareng ainsi que divers crustacés. Les œufs des saumons atlantiques peuvent être mangés par des canards et des saumons atlantiques. Certains oiseaux, en particulier le grand harle, le martin-pêcheur d'Amérique et le cormoran à aigrettes, ainsi que certains poissons, y compris le saumon atlantique, la truite, l'anguille et l'achigan à petite bouche, se nourrissent d'alevins et de tacons de saumon atlantique. Lorsqu'ils sont menacés par des prédateurs, les juvéniles s'immobilisent, comptent sur l'homochromie ou se cachent rapidement. Durant leur descente vers la mer, les saumoneaux peuvent être la proie de cormorans et d'autres oiseaux, de phoques et de divers poissons. En haute mer, les saumons sont la proie de poissons, d'oiseaux et de phoques. Les saumons adultes qui retournent vers leurs rivières natales peuvent être la proie de phoques. En eau douce, le saumon atlantique fait compétition à ses conspécifiques et à d'autres espèces, en particulier d'autres salmonidés, pour les ressources. Il parvient à éloigner l'omble de fontaine et la truite arc-en-ciel en eaux troubles, mais celles-ci lui livrent une plus forte compétition en eaux calmes. En hiver, les juvéniles ont besoin pour s'abriter durant le jour de cavités rocheuses, qui peuvent faire l'objet d'une intense compétition interspécifique et intraspécifique. Il n'y a pas eu d'études expérimentales sur les interactions biotiques entre le saumon atlantique et d'autres espèces dans l'océan. Il est peu probable que le flux d'éléments nutritifs provenant du saumon atlantique contribue beaucoup à la productivité en eau douce.

INTRODUCTION

The Atlantic salmon (*Salmo salar*) occupies marine and inflowing fresh waters of the North Atlantic Ocean. Most Atlantic salmon populations are anadromous, with spawning and early growth occurring in stream habitat, and rapid growth to adult size occurring in the sea. Populations which complete their life cycle in fresh water also exist, including those which occupy streams at the juvenile stage and grow to adult size in lakes.

During this complex life cycle Atlantic salmon interact with a variety of organisms as predators, as prey, and as competitors. This paper reviews Atlantic salmon feeding behaviour, prey, predator relations, and competitive interactions. North American and European populations of Atlantic salmon have broadly similar ecologies. This review draws from literature on both sides of the Atlantic, although North American sources are preferentially cited where available.

ATLANTIC SALMON AS PREDATORS

Fresh water

Atlantic salmon begin their life as yolk-sac larvae, which derive their nutrition from the marine feeding of their mothers (Doucett et al. 1996). Subsequently, Atlantic salmon obtain nutrition from their own feeding, whose intensity follows marked seasonal and diel cycles which vary according to life phase (Fig. 1).

Juvenile salmon feed most heavily in spring. Simpson et al. (1996) and Simpson and Thorpe (1997) found that appetite of parr in experiment tanks peaked in May, and subsequently declined throughout the summer. Bacon et al. (2005) reported that most growth of wild parr in Scotland occurred between early April and the end of June, although growth continued through the summer at a slower pace. Seasonal feeding rhythms may also be influenced by maturation schedules. Metcalfe (1994) found that parr in experimental tanks that were destined to smoltify the following spring showed intense appetite and very high feeding rates in September and October, despite declining water temperatures. The ensuing rapid growth enabled these fish to reach the threshold size for smoltification. In contrast, parr on a delayed maturation schedule showed a progressive decrease in appetite from July to late fall, even when food was available in abundance. Metcalfe (1994) also found that dominance status is linked to seasonal feeding schedules, because dominant fish were more likely to be members of the early maturation group. Juvenile Atlantic salmon continue to feed in winter, but at low levels (Fraser et al. 1995, Cunjak et al. 1998). Winter appetite is linked to nutritional status (Simpson et al. 1996) and appears to be directed to maintenance rather than to growth.

Atlantic salmon smolts feed intensively on their downstream journey to the sea (Hansen 1996). Adult salmon that have returned to fresh water for spawning generally do not feed (Hansen 1996), but there are exceptions. Johansen (2001) found that 45 of 133 stomachs of adult salmon in a Norwegian river contained food of freshwater or terrestrial origin.

Juvenile Atlantic salmon have traditionally been considered as diurnal in summer. However, recent studies have found much variation in diel cycles, often with substantial activity at night. Imre and Boisclair (2004) found that salmon fry in a tributary of the Saguenay River, Quebec, were equally active during day and night, while 1+ parr were active primarily at night. Gries et al. (1997) reported that parr of stocked origin in Vermont in August and September were active mostly at night. Amundsen et al. (2000) recorded stomach weights of juvenile salmon in subarctic Norway and Finland in August and September, a time of year when darkness prevails during night at the study latitude. Stomach weight peaked at 03:00, which suggests that the most intense feeding occurs at night. There were no pronounced diel fluctuations in food intake at other times of the ice-free season. In one river in northern Norway, Amundsen et al. (1999) found that feeding was most intense during the day among 0+ fish but most intense at night for older parr. Diel rhythms may vary with maturation schedules. Valdimarsson and Metcalfe (1999) found that parr destined to smoltify the following spring foraged mostly during the day, while parr destined to smoltify later foraged mostly at night.

In winter, juvenile Atlantic salmon occupy rocky shelters in the substrate during the day, and are active only at night (Cunjak et al. 1998). Occupancy of these shelters begins when the temperature reaches 10°C, and few fish remain visible in daytime when the water is cooler than 7°C (Fraser et al. 1995).

Feeding behaviour of juvenile Atlantic salmon is intimately linked with habitat use and social dominance status. Many, typically most, juvenile Atlantic salmon establish home ranges in stream riffle habitat which they defend against inter- and intra-specific competitors. These fish use their large pectoral fins as vanes to help them hold station on home rocks. When a food particle passes overhead, they dart upward, seize it, and return to the home rock (Wankowski and Thorpe 1979, Enders et al. 2005). Other feeding methods include head jerk feeding, where the head is snapped from side to side to seize prey particles (Wankowski and Thorpe 1979), and feeding on benthic prey (Armstrong et al. 1999). When food is concentrated, such as at the bottom of a falls, juvenile salmon may exhibit a school-type social structure, and feed together without territoriality (Wankowski and Thorpe 1979). In some areas, lakes provide important habitat for salmon parr (Dempson et al. 2004). Night-time feeding methods are not well studied in juvenile salmon. Valdimarsson and Metcalfe (1999) reported that juvenile salmon foraged at night at low light levels, and Heggens and Dokk (2001) found that night-feeding juvenile salmon held positions in areas of lower current flow, which contrasts to the high current stations typically occupied during the day.

Size of prey taken by juvenile salmon increases with the size of the salmon, although the maximum prey size is much less than the width of the salmon's mouth (Keeley and Grant 1997). Vignes (1998) reported that the mean length of benthic prey as a percent of salmon length varied from 1.9% to 3.5%, with a maximum of 5.7%.

Juvenile Atlantic salmon are opportunistic predators of aquatic invertebrates (Gibson 1993), especially those drifting at the surface. The most important prey are insects at the larval, nymph, or adult stage. Major prey groups include Ephemeroptera, Plecoptera, Trichoptera, Chironomiidae, and Coleoptera (Elson 1941, Gibson and Cunjak 1986, Hansen 1996). Parr in the Miramichi consume Atlantic salmon eggs at the time of spawning (Cunjak and Therrien 1998).

Some prey of juvenile salmon are terrestrial organisms that fall into the stream (allochthonous food) and some are of aquatic origin (autochthonous food). Isotope studies on the Catamaran Brook in New Brunswick indicate that most (85%) food in headwater reaches is allochthonous, but that allochthonous sources contribute only 36-52% of food in downstream areas (Doucett et al. 1996).

During their downstream migration smolts eat aquatic invertebrates, particularly insects, including Tricoptera, Ephemeropatra, Plecoptera, Simuliidae, and Culicidae (Hansen 1996, Johnson et al. 1996). Johnson et al. (1996) found that invertebrates of terrestrial origin were the main food sources for wild and hatchery-reared smolts trapped at dams on the Merrimack River, Maine.

Marine waters

After juvenile salmon enter the sea, their growth rates increase dramatically (Fig. 1). Post-smolt Atlantic salmon and non-maturing salmon of older ages feed intensively in spring and summer. Dutil and Coutu (1988) reported that the rate of increase in mean size of post-smolts sampled in the northwestern Gulf of St. Lawrence slowed in mid-September, suggesting a decline in feeding rate at that time. Fish in this study were not individually marked, so that different populations may have been sampled at different times. Hence the change in mean size does not necessarily represent the growth rates of individual fish. Salmon appear to continue feeding throughout the winter, although less intensively than during warmer periods. Lear (1972) found food in salmon stomachs taken in the northwest Atlantic throughout his sampling period (May to November). In the northeast Atlantic, 78% of stomachs contained food in February-March and 53% contained food in November-December (Jacobsen and Hansen 2000).

After the year of sea-entry, feeding and growth rates are closely linked to maturation schedules. Salmon that are destined to remain at sea for at least another year continue to feed heavily, but maturing fish stop or greatly decrease their feeding, so that fish sampled as they approach their native rivers

generally have empty stomachs (Lear 1972, Jacobsen and Hansen 2000). Fasting salmon on their return migration do not feed even when they pass through high densities of suitable prey (Sturlaugsson 2000). In tank experiments, Kadri et al. (1995) found that female salmon tended to cease feeding after lean body mass reached a certain threshold. The feeding status of late-run salmon which remain at sea in the summer prior to river entry is not well known. Cairns (2003), on the basis of stomach records and scale circuli patterns, suggested that these fish stop feeding in the spring and continue to fast in their remaining time at sea.

On the basis of gillnet catch rates, Dutil and Couto (1988) suggested that post-smolts are more active at dawn and dusk than in the middle of the day, but these authors also acknowledged that low mid-day catch rates may have been due to better net avoidance in the brightest part of the day. Holm et al. (2003) found that post-smolts were near the surface both day and night in summer in the Norwegian Sea. According to Hislop and Shelton (1993), marine-phase salmon feed near the surface at night. Reddin et al. (2004) fitted kelts with data storage tags as they exited Newfoundland rivers. Temperatures recorded by the tags showed no consistent diurnal rhythm, although some fish occupied warm water (indicating the surface layer) at night. Large scale diving behaviour, as indicated by sharp variations in water temperatures, occurred in late June and early July. Dives to deep layers may have been feeding forays, followed by return to the surface layer where warm temperatures speed digestion. Sturlaugsson (1995) captured adult Atlantic salmon returning to an Icelandic sea ranch operation, fitted them with data storage tags, released them at sea, and caught them again at the ranching stations. These fish spent most of the time close to the surface but dives also occurred, during both day and night. It is not clear if these dives were related to feeding as homing salmon usually do not feed and the fish lost weight during the experiment.

Marine-phase Atlantic salmon are primarily pelagic and mid-water feeders (Reddin 1985, Hansen et al. 2003). Fish are generally swallowed tail-first (Sturlaugsson 2000), which suggests that salmon pursue individual prey that seek to escape by rapid swimming. However, filter feeding also occurs, as indicated by visual observations of salmon rapidly swimming through fish larvae with jaws agape (Sturlaugsson 2000). The same author also cited high numbers of small invertebrate prey in stomachs as evidence for filter feeding.

Most prey of marine-phase salmon is less than 10 cm long, but prey longer than 20 cm is also taken (Hislop and Shelton 1993). The optimal width of prey is 2.2 to 2.6% of the salmon's body length (Mills 1989). Sturlaugsson (1994) found that post-smolts consumed prey with widths between 0.3 and 4.7% of their body length. In general, larger salmon take larger prey (Hansen et al. 2003).

Prey records of marine-phase salmon have been tabulated by Hislop and Shelton (1993). Post-smolts eat mostly invertebrates as they pass through estuaries, although diet may vary greatly among sites and among years (Levings et al. 1994). Diet often includes a substantial component of terrestrial insects, as well as crustaceans and small fish (Hislop and Shelton 1993, Jacobsen and Hansen 2000, Hansen et al. 2003, Rikardsen et al. 2004). Post-smolt diet in coastal waters includes sand lance and other small fish, various fish larvae, euphausiids, amphipods, copepods, and crab larvae (Hansen et al. 2003, Lacroix and Knox 2005). Piscivory is the main feeding mode for post-smolts of 25 cm or more (Hislop and Shelton 1993). Fish, particularly capelin, sand lance, and herring, are the principal foods of marine-phase salmon in waters off eastern Canada (Lear 1972, Reddin 1985). Other foods include small fish (including *Paralepis*) and crustaceans (particularly amphipods). In the northeast Atlantic, invertebrates play a greater role in salmon diet than they do in the northwest Atlantic (Jacobsen and Hansen 2000). Diet in the northeast Atlantic includes amphipods, euphausiids, herring, capelin, redfish larvae, blue whiting, lanternfish, sprat, cod, smelt, and *Paralepis*.

A small minority of returning adults feed as they enter their native rivers; diet is exclusively fish. In the case of early-run salmon, diet may include outgoing smolts (Sturlaugsson 2000).

ATLANTIC SALMON AS PREY

Fresh water

Cunjak and Therrien (1998) estimated that Atlantic salmon parr (particularly precocious males) consumed about 6% of Atlantic salmon eggs spawned in Catamaran Brook, New Brunswick. The common merganser preys on the eggs of Pacific salmon (Munro and Clemens 1937). This piscivorous duck (known as the goosander in Europe) breeds in much of the spawning range of the Atlantic salmon in North America, and in the northern part of the European spawning range. Chaput and Cairns (2001) suggested that predation by birds and fish on Atlantic salmon eggs is likely a common phenomenon. Munro and Clemens (1937) believed that most Pacific salmon eggs taken by mergansers had drifted downstream and had never been incorporated into the redd. Such eggs would probably not have hatched even in the absence of predation. It is not known to what extent predation by fish and birds of Atlantic salmon eggs targets eggs in the redd which would otherwise have a good chance of hatching, or eggs outside the redd which would have little chance of hatching.

A wide variety of predators feed on juvenile Atlantic salmon, but the best documented predation is by birds, particularly the common merganser, the belted kingfisher, and the double-crested cormorant (see compilation by Cairns 1998). Predators of Atlantic salmon fry include Atlantic salmon parr, brown trout, brook trout, smallmouth bass, American eels, great blue herons, spotted sandpipers, and greater yellowlegs (Table 1). Parr and smolts are consumed by American and European eels, brown trout, smallmouth bass, striped bass, burbot, and pike (Elson 1941, Godfrey 1957, Piggins 1958, Mills 1989, Baum 1997). Predators of juveniles (fry, parr, smolts) include mink, great blue herons, kingfishers, red-breasted mergansers, barred owls, and seals (Piggins 1958, Heggenes and Borgstrom 1988, Anthony 1994). In Maine, striped bass are a major predator of smolts as they exit from the tailraces of hydro dams (Blackwell and Juanes 1998).

Bioenergetic models estimate that common mergansers and belted kingfishers harvest from 21% to 45% of juvenile salmon in Maritime rivers in each juvenile year (age 0+ to 2+) (Cairns 2001a). However, analysis of historic culling experiments provides no evidence that a reduction in merganser and kingfisher numbers leads to increased juvenile salmon populations (Cairns 2001a). Mortality due to mergansers and kingfishers therefore appears to be compensatory rather than additive.

Pike ate an estimated 10% of the smolt run on the River Bran, Scotland (Mills 1989). Blackwell (1996) estimated that double-crested cormorants removed 7% of hatchery-reared smolts as they descended rivers towards the sea. There is widespread evidence of population increases in gulls and cormorants, which are potential smolt predators (Cairns 2001b).

Hawkins et al. (2004) showed that newly-hatched Atlantic salmon innately recognize the odor of pike as indicating a predatory threat. Feeding activity of juvenile Atlantic salmon may be suppressed by the presence of predators. In tank studies, Gotceitas and Godin (1993) found that juvenile salmon stopped feeding for less than a minute when a brook trout model was presented, and for several minutes when a kingfisher model was presented. Predator suppression of feeding activity also occurs in the wild, as indicated by Dionne and Dodson (2002) who used a common merganser replica as a predator model.

In the presence of a predation threat Atlantic salmon parr either freeze or dash for cover (Hawkins et al. 2004). Parr that freeze depend on cryptic coloration to avoid detection. Atlantic salmon parr can change colour to some degree to blend with the background (Donnelly and Whoriskey 1993). In winter juvenile salmon shelter in rock cavities during the day, which is viewed as an adaptation to reduce predation risk from warm-blooded predators at a time when the salmon's swimming performance is depressed by cold water (Valdimarsson and Metcalfe 1998).

Adult salmon that have returned to the river to spawn are too large to be taken by most predators. Some predation may occur from otters, and from seals that venture into the lower reaches of rivers (Table 1).

Marine waters

As Atlantic salmon smolts enter the sea they encounter higher salinity and new predator fields. Jarvis (1989) reported that osmotic stress during the fresh-salt transition impaired the ability of smolts to avoid predation. Handeland et al. (1996) tested this effect with cod as a predator, and found that predation losses increased when smolts were subject to abrupt salinity shifts. Osmotic stress may therefore contribute to the substantial predation mortality reported in some areas for salmon that have newly arrived in marine waters.

Outgoing smolts may be eaten by returning adult salmon, cod, saithe, sea trout, eels, double-crested cormorants, common and red-breasted mergansers, red-throated loons, gulls, and seals (Table 1; Anthony 1994, Feltham 1995, Sturlaugsson 2000, Svenning et al. 2005, Dieperink et al. 2002, Hansen et al. 2003). Most quantitative investigations of smolt survival are from the northeast Atlantic. Feltham (1995) estimated that common merganser predation removed 3-16% of smolt production in a Scottish river. Dieperink et al. (2002) tracked downstream movement of smolts in a Danish river with radio tags and determined that predation was light in the river, but was intense in the first few hours after sea entry, with major losses to gulls and cormorants. Larsson (1985) estimated that predation removed at least 50% of smolts from Swedish study sites before they reached the Baltic Sea. In Norway, Hvidsten and Mokkelgjerd (1997) obtained an adult return rate from smolt stocking at sea that was three times higher than the return rate from river stocking. They interpreted these findings as evidence for heavy predation in waters near the river mouth, which the at-sea stocking bypassed. However, some studies indicate low predation impact in the days after river exit. Svenning et al. (2005) found that only two of 2,308 otoliths recovered from common merganser stomachs at a Norwegian river mouth were from Atlantic salmon. Lacroix et al. (2005) reported a survivorship of at least 71-88% for smolts leaving Passamaquoddy Bay to the open Bay of Fundy.

Cairns and Meerburg (2001) examined the hypothesis that sea-pens for cultured salmon attract predators, thereby increasing predation on out-going smolts that pass near the pens. Seal surveys show no evidence of concentrations near sea-pens (Cairns and Meerburg 2001). Most of the small number of losses of out-going smolts leaving Passamaquoddy Bay for the open Bay of Fundy occurred in the vicinity of salmon farms, but causes of these losses were not determined (Lacroix et al. 2004).

Fish (in particular gadoids, Hansen et al. 2003) that feed heavily on salmon that have just left their natal rivers presumably also eat salmon in the open sea. Atlantic salmon have been found in stomachs of skate, halibut, ling, cod, porbeagle, Greenland shark, and pollock (Wheeler and Gardner 1974, Mills 1989, Hislop and Shelton 1993, Hansen et al. 2003).

Grey, harp, and harbour seals, common murres, and northern gannets are documented predators of post-smolt and Atlantic salmon in North America (Table 1), but records of predation events are very sparse (except for the northern gannet, see below). Investigation of predation on Atlantic salmon in the open sea is hampered by their rarity. Because salmon are a minute fraction of total prey biomass in the North Atlantic, they are likely also to be a minute fraction of predator diets. Cairns and Reddin (2000) calculated that, if the major seal and bird predators consumed 100% of a post-smolt cohort, salmon would only be 0.04% of the diet of these predators. This means that the amount of predation on Atlantic salmon cannot be reliably estimated without impractically large sample sizes.

Cairns and Reddin (2000) calculated windows of Atlantic salmon vulnerability to seal and seabird predators in the Northwest Atlantic, based on predator and prey migration patterns, salmon growth rates, and the maximum prey size the predator is capable of taking. Seals are able to eat Atlantic salmon of all sizes, so salmon growth does not close the vulnerability window to seal predation. However, vulnerability varies with seal migrations, particularly of harp and hooded seals which withdraw to the arctic during the summer. Vulnerability to seals may be highest when returning adults pass through estuaries on their way to natal rivers (Baum 1997, Middlemas et al. 2003), but vulnerability may vary geographically. In

Newfoundland, harbour seals frequent mouths of salmon rivers in the southern Avalon Peninsula and harp seals frequent mouths of salmon rivers on the northeast coast, but on west coast rivers the potential for seal predation appears light (Sjare and Reddin 2002). Carter et al. (2001) found that seal mortality in a Scottish river was an order of magnitude less than mortality due to angling. Seabirds are constrained in the size of the prey they can take, and post-smolt salmon out-grow predator capability between mid-June and fall, depending on the species.

Some Atlantic salmon that return to rivers bear scars that appear to be due to seal attacks (Bonner 1982, Cairns 2003). Baum (1997) reported that 2% of adults returning to the Penobscot River in Maine had seal bites, and that the percent of scarred animals had risen in recent years. Cetaceans, including bottlenose dolphins, belugas, and possibly harbour porpoises, also consume marine-phase Atlantic salmon (Middlemas et al. 2003). Thompson and MacKay (1999) found that 19.5% of returning salmon in northeast Scotland were scarred, but they felt, on the basis of scar patterns, that most of the damage had been inflicted by odontocetes rather than by seals.

The northern gannet is a large plunge-diving seabird that occupies waters in the salmon's marine range on both sides of the Atlantic Ocean. Because of its specialization in near-surface prey, it appears to be particularly adept at taking post-smolt salmon. Gannet regurgitation samples obtained in August at Funk Island, off Newfoundland's east coast, were 0.29% salmon in 1977-1989 and 2.53% salmon in 1990-2000 (Montevecchi et al. 2002). Salmon consumed during August at this colony were an estimated 0.22% and 2.7% of total North American biomass of the cohort. Given that these estimates apply to only one month and one (of six) gannet colonies, predation impact by gannets on post-smolt salmon is potentially high. However, gannet diet at times other than August, and at colonies other than Funk Island, is too poorly known to determine if this is so.

Behavioural mechanisms which marine-phase Atlantic salmon use to reduce predation risk are not well known. Schooling is the main anti-predator strategy of pelagic fishes (Krause et al. 1998). Clustering of gillnet catches (Dutil and Couturier 1988) and observations of schools in Norway (Holm et al. 1992), Iceland (Sturlaugsson 1995) and in New Brunswick sea-pens (F. Whoriskey, pers. comm.) suggest that marine-phase salmon have at least some degree of natural schooling tendency. Low salmon numbers, particularly in the Bay of Fundy, could prevent marine-phase salmon from forming schools, and thereby increase their vulnerability to predation (Cairns 2001c, Lacroix and Knox 2005).

INTERSPECIFIC INTERACTIONS

Competition in fresh water

Atlantic salmon juveniles are territorial and competitive, and year-class abundance declines over time as a result of competition for limited resources (Chaput 2001). Juvenile Atlantic salmon in fresh water compete for resources with conspecifics and with other species, particularly other salmonids.

Fausch (1998) reviewed 17 experiments on interspecific competition between juveniles of Atlantic salmon and other species, and concluded that many studies lack proper replicates and controls. This casts some doubt on the extent to which findings from these studies can be generalized to other times and areas.

Because of their large pectoral fins, juvenile Atlantic salmon have a particular ability to hold position on the bottom in fast water (Gibson 1993). The basic pattern of juvenile salmon life in fresh water is to occupy areas in riffle habitat which they defend against other fish. This section refers to these areas as "home ranges" although "territory" is also used in the literature. Juvenile salmon may also use other types of stream habitat, including deep low-current waters (Gibson 1993) and lakes (Dempson et al. 2004).

Where Atlantic salmon share streams with brook trout, salmon displace the trout from riffle habitat (Gibson 1993). Atlantic salmon are less aggressive than trout in pools, and trout may limit salmon growth in that habitat (Gibson 1993). Pool-dwelling species such as percids and cyprinids may also limit Atlantic salmon numbers in slow waters. Working in Newfoundland, Gibson et al. (1993) found that salmon

biomass was higher in riffles and trout biomass was higher in pools. Salmon biomass was higher in the absence of trout. Gibson and Dickson (1984) found that Atlantic salmon juveniles showed enhanced growth in an otherwise fishless area of boreal Quebec, and also in a stream from which brook trout had been removed.

Laboratory and field experiments indicate that Atlantic salmon fry used the same variety of habitats when alone and when in the presence of rainbow trout, but 1+ salmon parr were constrained to riffle habitat in the presence of rainbows, which were highly aggressive towards the salmon (Fausch 1998).

Raffenberg and Parrish (2003) found no significant relations between survivorship of Atlantic salmon fry and abundance of brook and rainbow trout in 24 stream reaches in Vermont. Instead, fry survival was positively related to abundance of brook trout parr and to benthic food abundance. This suggests that the view that competition forces an inverse relation between trout and salmon populations may not be tenable on a geographic scale that encompasses a number of stream reaches.

The brown trout, native to Europe, has been introduced to numerous North American systems used by Atlantic salmon. Brown trout tend to use the margins of runs and pools where water velocity is lower, in contrast to riffle specialization by Atlantic salmon (Fausch 1998, Bremset and Heggenes 2001, Heggenes et al. 2002). Nevertheless there is overlap in types of habitat used by the two species (Heggenes and Dokk 2001).

Gibson and Cunjak (1986) reported that introduced brown trout in the Avalon Peninsula, Newfoundland, were largely segregated from Atlantic salmon by habitat choice and to some degree also by food habits. No negative effects by brown trout on salmon were demonstrated. European studies suggest that stocked Atlantic salmon show poorer growth and survival in the presence of brown trout, but these studies suffer from a lack of replication (Mills 1989, Fausch 1998).

Hojesjo et al. (2005) found that large brown trout dominated smaller Atlantic salmon in a stream channel, but that salmon food intake was nevertheless not suppressed because the salmon fed sneakily by darting into the trout's space.

Juveniles of both brown trout and Atlantic salmon are nocturnal in winter, and tend to occupy slower-flowing water than they do in summer (Heggenes and Dokk 2001). Harwood et al. (2001) found that in the presence of brown trout, wintering Atlantic salmon either shifted their habitat use into shallower water while remaining nocturnal, or became more diurnal.

Jones and Stanfield (1993) investigated the effects of exotic salmonines on hatchery-produced juvenile Atlantic salmon in a tributary of Lake Ontario. Atlantic salmon growth and survival significantly increased when Pacific salmon (particularly cohos), yearling rainbow trout, and brown trout were removed, suggesting that these introduced species may competitively suppress Atlantic salmon of hatchery origin.

American and European eels are sympatric with Atlantic salmon in much of their freshwater range on the west and east sides of the Atlantic, respectively. Elson (1941) reported that young eels eat largely the same food as young salmon, and argued that eels should be removed to favour the salmon. However, Mann and Blackburn (1991) found that eel diet is largely benthic invertebrates in contrast to the mid-water and surface prey of juvenile Atlantic salmon. These authors reported that eels did not have a measurable effect on juvenile salmon either through competition or predation.

Wintering juvenile salmonids require daytime shelters for survival, and such shelters may be subject to intense intra- and inter-specific competition if demand exceeds supply (Cunjak et al. 1998). Experiments with Atlantic salmon and brown trout revealed that prior residence was a major factor in determining shelter ownership, that the two species showed similar levels of aggression, and that neither species was able to consistently exclude the other from shelters (Harwood et al. 2002). Signal crayfish, native to North America west of the Rocky Mountains, have established introduced populations in many European

countries (Anon. n.d.). Griffiths et al. (2004) found that signal crayfish were very effective in excluding juvenile Atlantic salmon from shelters when these were in short supply.

Competition in marine waters

Because of the vast scale of the Atlantic salmon's ocean habitat, field experiments to measure competitive interactions with other species have not been conducted. As Levings (1994) pointed out, it is difficult to determine if salmonids compete for food with other species in the ocean because it is hard to establish whether the carrying capacity of marine areas is exceeded. This has not prevented authors from speculating on competitive interactions between marine-phase salmon and other species. Anthony (1994) suggested that Atlantic salmon compete against seals, because both seals and salmon eat capelin in the northwest Atlantic. Hansen et al. (2003) referred to statistical evidence of a negative relation between herring abundance and salmon marine survival in northwestern Europe. These authors speculated that competition for food might be a cause of this relation. Because biomass of biomass of marine-phase Atlantic salmon is very low (Cairns and Reddin 2000), intra-specific competition for food is unlikely to be significant.

Nutrient flux

Pacific salmon are a net importer of nutrients from marine to freshwater systems, and nutrient flux due to salmon contributes substantially to productivity in some watercourses (Wipfli et al. 2003). Nislow et al. (2004) calculated that Atlantic salmon in a Scottish stream are net exporters of nutrients from freshwater. These authors also calculated that nutrient flux to freshwater could become positive if return rates of salmon from the sea improved. Returning Atlantic salmon represent only about 1% of the total biomass of spawning anadromous fish entering the Miramichi River (Chaput 1995). It appears unlikely that nutrient flux due to Atlantic salmon significantly contributes to freshwater productivity.

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Table 1
Predators of Atlantic salmon in North America.

Salmon life stage	Predator	Region	Comments	Source
Fry	Atlantic salmon	Massachusetts	Fry were of hatchery origin	Henderson and Letcher 2003
Fry	Brook trout	Massachusetts	Fry were of hatchery origin	Henderson and Letcher 2003
Fry	Brown trout	Massachusetts	Fry were of hatchery origin	Henderson and Letcher 2003
Fry	American eel	New Brunswick		Godfrey 1957
Fry	Greater yellowlegs	Cape Breton Island		White 1939
Fry	Spotted sandpiper	Cape Breton Island		White 1939
Fry, parr	Smallmouth bass	Maine	Smallmouth bass is an introduced species	Baum 1997
Fry, parr, smolt	Great blue heron	Cape Breton Island		White 1939
Fry, parr, smolt	Brook trout	Cape Breton Island		White 1939
Parr	White perch	Cape Breton Island		White 1939
Parr	American eel	Nova Scotia		Elson 1941
Parr	Harbour seal	Waterford R., Nfld	Sight record, possibly a trout	Cairns and Reddin 2000
Parr	Common goldeneye	Cape Breton Island		White 1939
Juvenile	Double-crested cormorant	New Hampshire, Maine, Maritime Provinces, eastern Quebec	During smolt run: salmon were 17.3% of diet	Cairns 1998
Juvenile	Double-crested cormorant	New Hampshire, Maine, Maritime Provinces, eastern Quebec	Not during smolt run: salmon were 0.1% of diet	Cairns 1998
Juvenile	Common merganser	Maritime Provinces	Salmon were 27.2% of diet	Cairns 1998
Juvenile	Red-breasted merganser	Maritime Provinces	Salmon were 0.5% of diet	Cairns 1998
Juvenile	Belted kingfisher	Maritime Provinces	Salmon were 14.9% of diet	Cairns 1998
Smolt	Chain pickerel	Maine	Chain pickerel is an introduced species	Baum 1997
Smolt	Striped bass	Maine		Blackwell and Juanes 1998
Post-smolt	Harbour seal	Near Grand Manan I., NB	Tag recovery	B. Beck, in Cairns and Reddin 2000
Post-smolt	Common murre	Witless Bay, Nfld	Tag recovery	Montevecchi et al. 1988
Post-smolt	Northern gannet	Funk I., Nfld	Mean contribution of post-smolt to gannet diet in August ranged from 0% to 6.4% in 1977-2000.	Montevecchi et al. 2002
Small adult	Harp seal	St. Lawrence estuary		Beck et al. 1993
Small adult	Harp seal	Notre Dame Bay, Nfld		O'Connell et al. 1998
Adult	Grey seal	Anticosti I., Magdalen Is., Miramichi estuary	In some cases salmon might have been stolen from nets	Fisher and Mackenzie 1955, Mansfield and Beck 1977, Benoit and Bowen 1990
Adult	Grey seal	St. Marys Bay, Nfld	Sight record	Cairns and Reddin 2000
Adult	Grey seal	White Bear estuary, Labrador	Sight record	Cairns and Reddin 2000
Adult	Grey seal	Paradise estuary, Nfld	Sight record	Cairns and Reddin 2000
Adult	Otter	Cape Breton Island		White 1939
Adult	Bald eagle	Cape Breton Island		White 1939
Kelt	Harp seal	Twillingate, Nfld	Sight record	Cairns and Reddin 2000

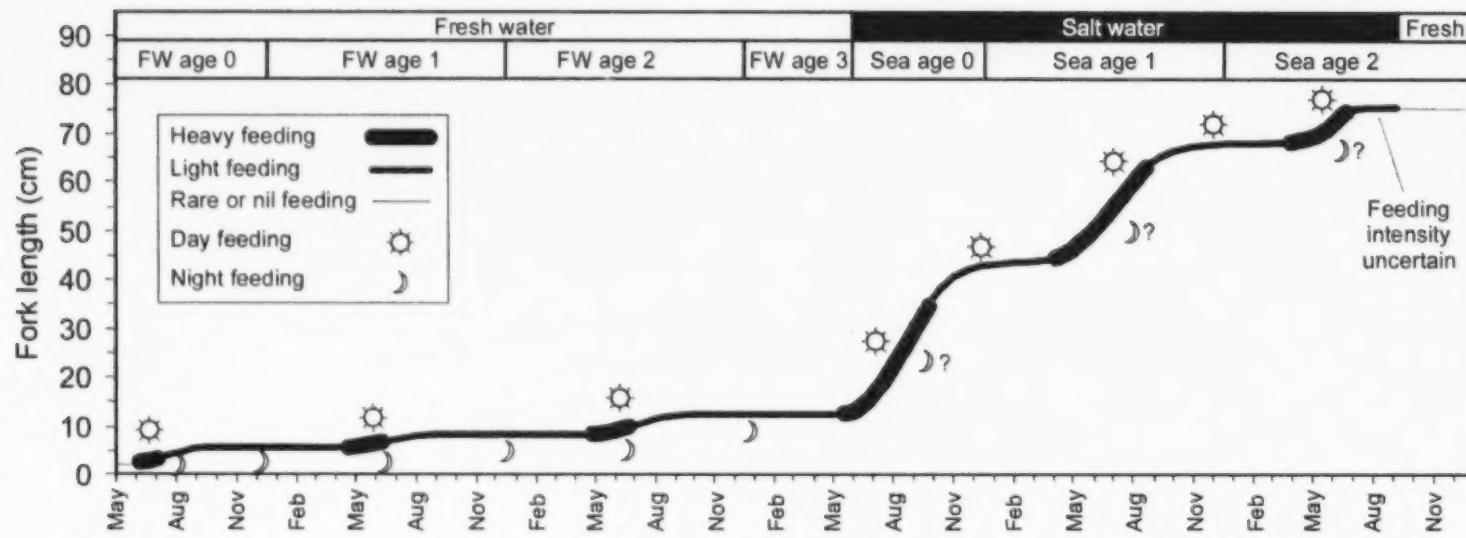


Fig. 1

Schematic summary of lifetime growth and feeding patterns of Atlantic salmon, based on sea exit at freshwater age 3 and river return at sea age 2. Freshwater growth curve from data in Randall and Chadwick (1986); marine growth curve from Cairns and Reddin (2000).

